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QUEEN NUMBER IN COLONIES OF SOCIAL HYMENOPTERA AS A KIN-SELECTED ADAPTATION

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Abstract. — Using a series of kin-selection models, I examine factors that favor multiple egg-laying queens (polygyny) in eusocial Hymenoptera colonies. One result is that there is a theoretical conflict of interest between the founding queens and their daughter workers over how many and which individuals should be the extra reproductives. Both castes should prefer their full sisters. Therefore, primary polygyny (multiple related foundresses) may favor queens while secondary polygyny (related queens added to mature colonies) may favor workers. Polygyny, itself, was found to be favored by high colony survivorship and low probability of queens contributing eggs to successive broods. Polygyne colonies, however, did not need to produce more offspring per brood to be selectively favored; they could be half as productive per brood as monogyne ones and still have higher lifetime fitness under some conditions. For reproductive data from eight ant species with both monogyne and polygyne colonies, the model generates results that are consistent with a kin-selection explanation of polygyny in all of them. It is proposed that queen number is an ecologically flexible trait that is influenced by a broad set of factors but is not necessarily linked to specific habitat types. Furthermore, neither polygyny nor monogyny may be reliably considered as the primitive or ancestral Hymenopteran social system. The optimal queen number within a species may evolutionarily increase or decrease, depending on the direction of environmental change.

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In the social Hymenoptera, many individual members of colonies produce no direct offspring but, instead, tend those of other colony members. Viable egg production is often found only in one specific caste of individuals, called the queens. The number of functional queens per colony, however, is a variable trait. Many species habitually have only one queen per colony (monogyny), while others have two or more (polygyny) (Wilson, 1971; Trivers and Hare, 1976). Furthermore, queen number can vary between colonies within a species (Elmes, 1980; Herbers, 1984; Nonacs, 1986). A stable social system with multiple functional queens appears to be an evolutionary dilemma. Individual queens could expect to produce more of their own offspring if they did not have to share resources with other queens. The workers should prefer to raise only their own mother's offspring and not tend more distantly related queens' progeny. Hölldobler and Wilson (1977) found that, among ants, polygyny tended to be associated with either short-lived nest sites or large, stable, patchily distributed habitats. This is, however, a proximate explanation and does not answer the ultimate question of the mechanism by which polygyny is favored, even if only within these limited ecological conditions.

Hypotheses for the evolution of polygyny have fallen into four broad (but not necessarily mutually exclusive) categories.

- 1) Kin selection (Wilson, 1974): colonies add related reproductives to prolong colony lifetimes. Therefore, although the members suffer initially reduced fitness, their lifetime inclusive fitness is increased. All members of the colony may not gain equally or at all through polygyny.
- 2) Mutualism (West-Eberhard, 1978*a*, 1978*b*): all members of a colony immediately gain through polygyny and need not be closely related. In a hierarchical society, dominant queens benefit from a larger and more efficient work force for their brood. Subordinates and workers benefit by occasionally usurping the dominants as egg layers or, through inclusive fitness, by assisting their possibly more productive relatives. Although all individuals within a colony need not have equal fitness, on average their fitness should be greater than or equal to that achieved by monogyny.
- 3) Colony or group selection (Oster and Wilson, 1978): polygyne colonies produce more total offspring or dominate habitats in such a manner that they are

avored even though the fitness of average individuals is higher in monogynous colonies.

- 4) Parasitism by queens (Elmes, 1973): newly mated queens invade or never leave colonies that already have queens. The invading queens gain in fitness because their reproductive output is on average greater than if they attempted to start their own nests. All other members of the colony suffer reduced fitness.

I develop models to examine whether polygyny can be explained by the first of the above mechanisms, namely kin selection. Kin-selective mechanisms have been hypothesized to be involved in the origin of eusociality (Hamilton, 1964*a*, 1964*b*) and have become the dominant paradigm in explaining social Hymenopteran sex ratios (Trivers and Hare, 1976; Nonacs, 1986). The problem of polygyny should be amenable to a similar approach. My goals are 1) to identify which individuals should be favored to become polygynous queens and whether there are intercaste differences and conflicts over polygyny thresholds; 2) to quantify the effects of ecological factors on colony characteristics, such as survivorship, and predict the conditions under which polygyny is adaptive; and 3) to test the above kin-selection predictions with the observed data for polygynous eusocial Hymenoptera.

Polygyny and Kin Selection in Brood Production

For the following model, I initially assume that a colony consists of one queen (α) and her worker daughters, all of whom are full sisters. This colony must decide whether to add or retain extra reproductives (β queens). I assume that any given β queen has a minimal chance of successfully founding a new colony by herself and will, on average, produce more offspring as part of a polygynous association. Therefore, if allowed, β queens will always join established colonies. The existing colony members are likewise assumed to expect little future gain through exclusion of any given queen. Therefore, their decisions will be modeled by cost/benefit analyses in relation to the existing colony's sexual production. In this model, the choice involves adding either the queen's

TABLE 1. The coefficients of relatedness of the offspring of the α queen, α 's sisters, and α 's daughters to the singly mated α queen and to her daughter workers. Either α 's sister or α 's daughter would be a β queen.

Of:	Coefficients of relatedness	
	To:	
	α Queen	Unmated worker
α queen's son	0.500	0.250
α queen's daughter	0.500	0.750
α 's full sister's offspring	0.375	0.1875
α 's daughter's offspring	0.250	0.375

full sisters (workers' aunts) or the queen's daughters (workers' full sisters). These are the closest kin available and, therefore, are most likely to be the individuals added as new queens.

If there is no cost in lost reproduction to the α queen, both the α queen and her workers should favor adding related egg-layers. If, however, the presence of β queens reduces egg production by the α queen, addition of queens should be favored only if β queens more than offset this lost production. If all queens are assumed to contribute equally to reproduction (i.e., each produces $1/Q$ proportion of future offspring), the following relationship must be true for polygyny to be beneficial for a particular class of colony members:

$$N_m G_\alpha < \frac{N_p [G_\alpha + G_\beta (Q - 1)]}{Q} \quad (1)$$

where N_m and N_p are the numbers of reproductives produced by monogynous and polygynous colonies, respectively, Q is the total number of queens (both α and β), and G_α and G_β are the average coefficients of relatedness between the offspring of α and β queens, respectively, and the class of colony members. For each type of queen, this would be the sum of the proportions of male and female offspring, weighted by the coefficients of relatedness (Table 1).

Rearranging Equation (1) produces

$$\frac{N_p}{N_m} > \frac{Q G_\alpha}{G_\alpha + (Q - 1) G_\beta}, \quad (2)$$

or the threshold ratio of sexual production required for polygyny to be favored by colony members. The α queen and workers will not have identical polygyny-favoring

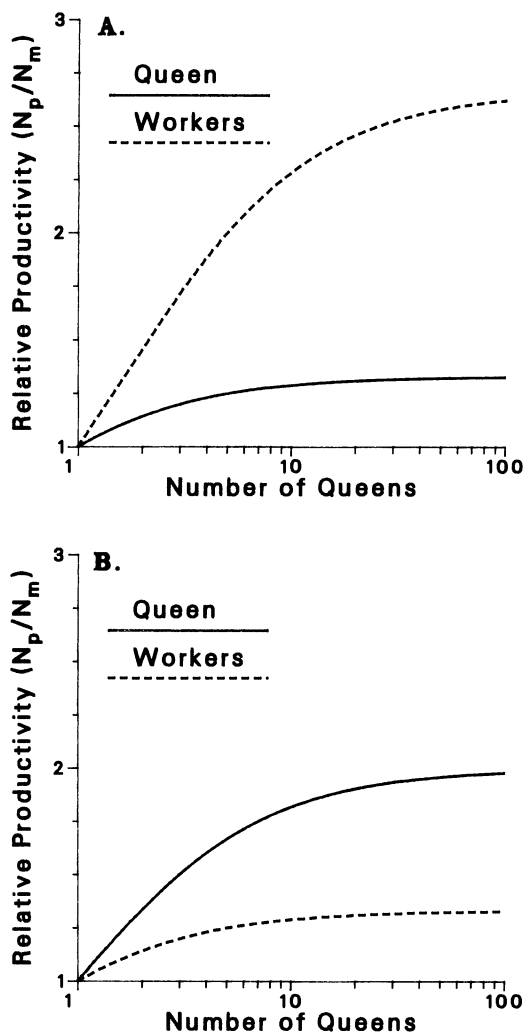


FIG. 1. Polygyny thresholds for the queen and her workers. The curves indicate the relative increase in colony productivity (N_p/N_m) required for polygyny to be favored over monogyny for a given queen number (Q) under the assumption that all queens produce equal numbers of males and females. A) All queens are full sisters, and β queens are aunts to the workers; B) the α queen is the mother of all the β queens, who are full sisters of the workers.

thresholds, because the possible β queens are not equally related to them (Table 1). Figure 1 illustrates the case in which males and females are produced in equal numbers (which is often true for ants [Nonacs, 1986]). While neither queens nor workers are more prone to favor polygyny, they do differ as to who they favor as the β queens. For each caste, polygyny is most favored when their sisters become β queens. This suggests that

the ontogeny of polygyny may indicate whether it is influenced more by queens or workers. Polygyny can be primary, in which a group of queens found a colony cooperatively (pleometrosis) and all or several survive into colony maturity. Alternately, polygyny can be secondary, in which queens are added to monogynous colonies during maturation. The above model predicts that primary polygyny is likely to be favored by queens (Fig. 1A) and that secondary polygyny is likely to be favored by workers (Fig. 1B).

In polistine wasps, polygyny appears to favor queen interests. Polygyny is predominately primary, and queens appear to preferentially associate with sisters (Klahn, 1979; Ross and Gamboa, 1981; Post and Jeanne, 1982; Klahn and Gamboa, 1983). However, most *Polistes* have annual life cycles, and sexuals are only produced at the end of the year (Wilson, 1971) so that workers do not often have the option of replacing aunts with reproductively equal sisters. In ants, although pleometrosis appears to be common, it is as likely to be explained by mutualistic advantage as by kin selection (Rissing and Pollock, 1987a, 1987b). It is apparent, though, that primary polygyny is often unstable. Aggression between queens or their daughter workers eventually leads to monogyny (Waloff, 1957; Baroni-Urbani, 1968; Bartz and Hölldobler, 1982; Fletcher and Blum, 1983; Hölldobler and Carlin, 1985; Rissing and Pollock, 1987a). The model predicts that disruption of primary polygyny, when queens are related, should be initiated by workers, because they are less likely to favor retaining the extra queens. In the above studies, however, whether queens or workers are mainly responsible for reductions in queen numbers appears to vary across species.

One problem faced by a worker who would kill pleometrotic foundresses is that to maximize fitness, she should not eliminate her mother. This does not mean that workers must discriminate their relatedness to all the foundresses. Forsyth (1980) proposed a possible mechanism that does not require genetic recognition. Most workers should be daughters of the most productive queens and by eliminating the least productive queens, the average worker will increase its

relatedness to the next brood. In essence, they are increasing the proportional representation in future broods of the queen who is most likely to be their mother. Bartz and Hölldobler (1982) and Fletcher and Blum (1983) found that workers eliminated queens based on their productivity.

In perennial Hymenoptera, stable polygyny has been assumed to be predominately secondary (Oster and Wilson, 1978), because primary polygyny has never been conclusively demonstrated, while several cases of colonies becoming secondarily polygynous by retention of fertilized daughter queens have been documented (Janzen, 1973; West-Eberhard, 1973; Ross and Visscher, 1983). Although this assumption needs to be tested by following ontogenies of colony maturation in routinely polygynous species, the balance of this paper considers only secondary polygyny.

Sequential Addition of Queens

The previous model predicted the increases in sexual production required to favor polygyny for given numbers of added queens. If a monogynous colony adds queens sequentially during the season, rather than in groups, the threshold for addition of queens, as measured by increases to colony sexual production, may not be constant. For a colony already having Q queens, the α queen and her workers will favor the addition of another queen when the gain in sexual production through the additional queen (N_g) exceeds the loss in sexual production in the colony's Q queens (N_l) such that

$$N_g G_\beta > \frac{N_l [G_\alpha + G_\beta (Q - 1)]}{Q} \quad (3)$$

or

$$\frac{N_g}{N_l} > 1 + \frac{\frac{G_\alpha}{G_\beta} - 1}{Q} \quad (4)$$

The equivalent relationship for a β queen is

$$\frac{N_g}{N_l} > 1 + \frac{\frac{G_\alpha + 0.5}{G_\beta} - 2}{Q}, \quad (5)$$

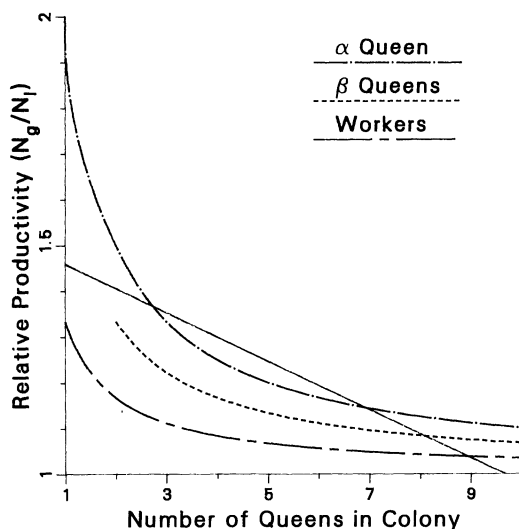


FIG. 2. Thresholds for sequential queen addition. The curves represent the relative increase in sexual productivity (N_g/N_l) required for the addition of a queen to be favored by the α queen, a β queen, or α 's daughter workers when Q queens are already present. The solid line is a hypothetical productivity function of queen number. The intersections with the thresholds are the optimal queen numbers for the α queen, β queens, and workers, which are 7, 8 and 9, respectively, in this case.

because their own expected reproduction must be separated from the other β queens. From (4) and (5), it is apparent that the threshold for addition of a queen becomes progressively smaller as queens are added.

For the queen-addition thresholds depicted in Figure 2, I have assumed that the queen to be added is the worker's full sister and that all queens produce equal numbers of males and females. It is evident that the workers will always favor adding queens before any of the queens do. Moreover, this suggests that, for any given N_g/N_l function of queen number, workers will tend to add more queens to the colony than is optimal from any resident queen's standpoint. Conflicts over preferred queen numbers may be expressed by behavioral differences across the castes in that queen-queen interactions may be more hostile and aggressive than are queen-worker interactions.

Polygyny and Lifetime Fitness

The previous models predict the conditions needed to favor polygyny in the production of a single brood. This necessitates

that polygyny must increase annual offspring production ($N_p > N_m$ and $N_g > N_1$). However, many Hymenopteran colonies are perennial and produce several broods over many years. Therefore, for many species, the above model may be too restrictive on the conditions favoring polygyny. In developing the following model of the conditions required for workers to favor polygyny, I make six assumptions.

- 1) Once a monogyne colony produces its first brood, it has the option of readmitting $Q - 1$ daughters to serve as β queens. The number of queens (Q) will be kept constant at the end of each brood-producing cycle by replacing lost queens with new queens from that brood.
- 2) All queens present when a sexual brood is raised have contributed equally to it, and each queen has an equal probability of being present (l_Q) to contribute eggs to the next brood. (This is not strictly a measure of queen survivorship; I will discuss how factors other than mortality may prevent queens from contributing eggs in the next section.) Therefore, the probability that at least one queen is present to produce eggs for a cycle equals $1 - (1 - l_Q)^Q$. A colony with no fertile queens produces no offspring and dies.
- 3) Entire colonies can be destroyed by predators or environmental disturbances. Therefore, a colony has a probability of surviving to produce the next brood (l_c) that is independent of queen survival or presence. Arbitrarily, in this model, no colony survives past the 10th brood ($i = 1-10$).
- 4) Both sexes are produced in equal numbers.
- 5) After each brood, $Q(1 - l_Q)$ new queens are admitted to replace those which have been lost over the last breeding cycle. This means that by the 10th brood produced under polygyny there may be 11 generations contributing progeny. If all

queens are assumed to mate only once, the average relatedness ($\bar{r}$) of any given future brood to the original workers will be a weighted average of the contributions of their mother (P1), sisters (F1), and all subsequent generations (FJ, $J = 2-10$), such that

$$\bar{r}_i = 0.5P1_i + 0.375 \left(F1_i + \sum_j \frac{FJ_i}{2^{J-1}} \right). \quad (6)$$

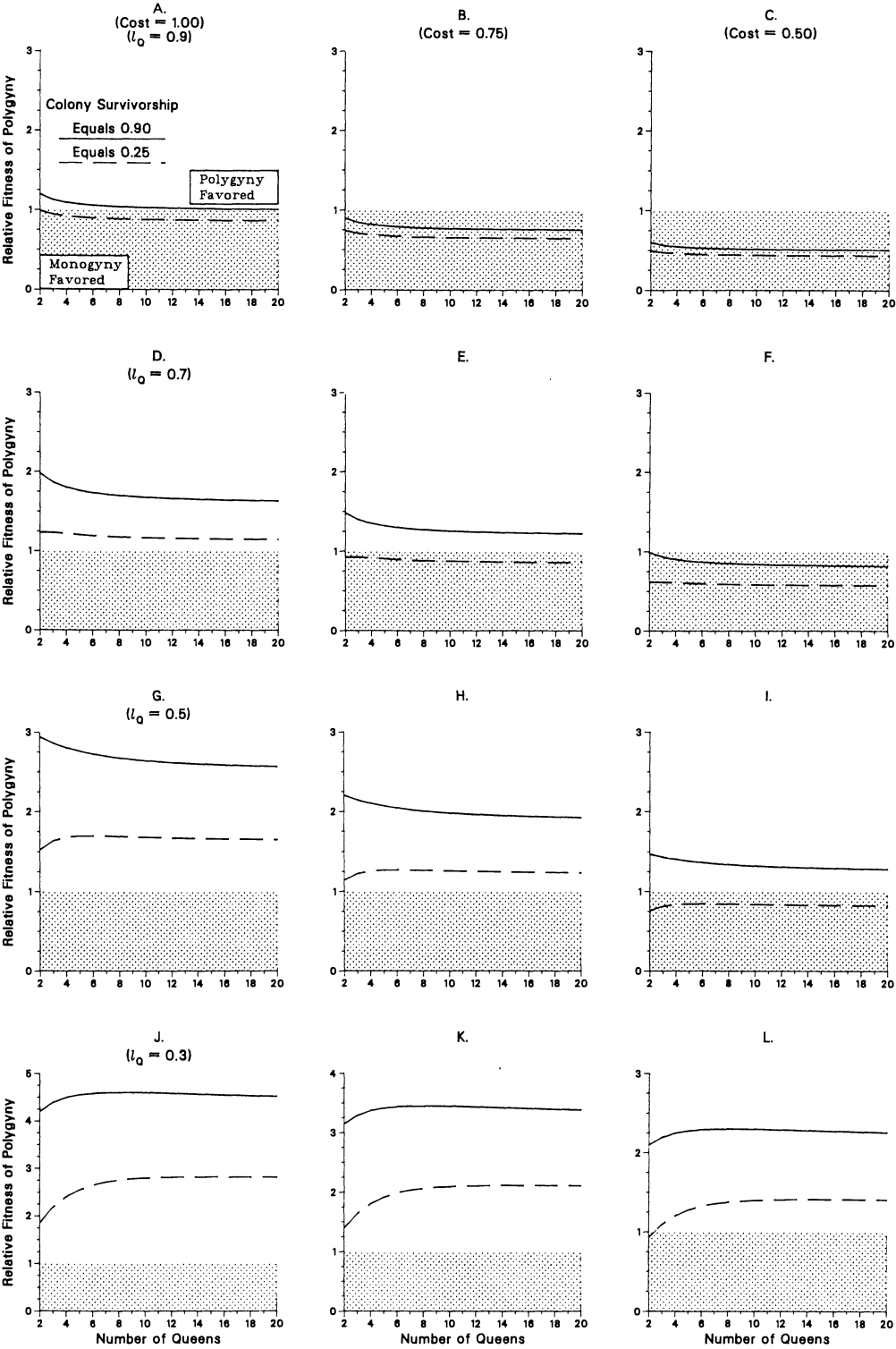
The value of $\bar{r}$ will change across broods. In the first brood, ($i = 1$), $P1_1 = (1/Q)$, $F1_1 = (Q - 1)/Q$, with all $FJ_1 = 0$. For all other broods ($i = 2-10$), $P1_i = P1_{i-1}l_Q$, $F1_i = F1_{i-1}l_Q + P1_{i-1}(1 - l_Q)$, and $FJ_i = FJ_{i-1}l_Q + F(J - 1)_{i-1}(1 - l_Q)$.

- 6) If the colony survives and has a fertile queen, it produces a brood of cN_m offspring, where c = cost (as a proportional reduction of the sexuals/brood) to a colony of being polygyne. Unlike the previous model, productivity of polygyne colonies in this model is restricted so as not to exceed that of monogyne colonies ($c = 1$) or to have an actual cost in reduced brood-rearing efficiency ($c < 1$). Costs could arise from maintaining extra (and nonworking) queens or from the possible loss in efficiency due to aggression between queens or sister cohorts of workers. Polygyne colonies have been shown to be able to produce more eggs, although it is unclear whether this eventually translates into more sexuals (Fletcher et al., 1980). Efficiency in performing colony tasks does not appear to increase with polygyny (Herbers, 1982). Therefore, the lifetime fitness of an original worker equals

$$cN_m \sum_i \{ [1 - (1 - l_Q)^Q] l_c^i \bar{r}_i \}. \quad (7)$$

In monogyne colonies, new queens are never admitted, and the foundress mates only once ($\bar{r}$ always equals 0.5), so lifetime fitness of an original worker is

FIG. 3. Colony lifetime fitness. The curves represent the fitness of polygyny relative to monogyny for a range of queen numbers (Q) and colony survivorship (l_c). In the shaded regions, monogyny is favored. The rows of figures correspond to four levels of probability for a queen contributing eggs to the next brood (l_Q), and the columns are three levels of cost for maintaining extra queens, as measured by the proportional reduction in the total sexual brood (c).



$$0.5N_m \sum_i l_Q^i l_C^i. \quad (8)$$

From the above equations, for any given combination of l_Q , l_C , and c , the optimal queen number from the workers' viewpoint can be determined. The graphs in Figure 3 show the benefits of polygyny relative to monogyny for a range of queen numbers [i.e., Eq. (7) divided by Eq. (8) for given Q values]. In general, the results show that polygyny is more likely to be selectively favored when the probability that a queen will contribute eggs to subsequent broods is low (comparisons within any column in Fig. 3), colony survivorship is high (comparisons of solid to dashed lines in Fig. 3), and sexual production per brood is not greatly decreased by polygyny (comparisons within any row in Fig. 3).

The results have several implications for the occurrence of polygyny. First, if the average queen is unlikely to contribute to many broods, polygyny is favored. There may be several factors that decrease the likelihood of queens contributing to multiple broods. Queens may, on average, have short lifespans. Therefore, colonies may need to add queens after brood production to insure that some survive for subsequent egg production. Queens can be lost in ways other than death. In species that nest in ephemeral sites or move frequently, the colony may be inadvertently split. Polygyny may increase the probability that any splinter group will contain at least one reproductive. A similar situation exists when a single colony inhabits several adjacent nest sites (polydomy). Workers in polydomous colonies may move from site to site, but access to eggs may be facilitated by each nest site having its own polygyne queens. Pamilo and Rosengren (1984) found that polygyny often occurred in conjunction with polydomy in several species of *Formica* ants.

Although several of the above factors have been found to be correlated with polygyny (Hölldobler and Wilson, 1977), a cause-and-effect relationship may be difficult to establish clearly. The above models predict that short-lived queens favor colonial polygyny. However, it may also be argued that polygyny selects for short-lived queens. When β queens are added, they are initially sisters of the workers (Fig. 1B). Over time, the orig-

inal workers die and are replaced by the polygyne queens' offspring. This changes the relatedness within the nest to a situation more like that in Figure 1A, in which most of the queens are aunts to the average worker. As with the initial foundress associations, there would be great selective advantage for any cohort of sister workers to replace distantly related queens with their own full sisters. Forsyth's (1980) model for queen killing is extendable to queen turnover as well. If workers replace the least reproductive queen with one of the brood, their average relatedness to future offspring would rise. Such worker behavior may result in selection on queens to maximize present reproduction at the expense of future reproduction and lifespan. It may be predicted that, in polygyne species, the average queen's lifespan should approximate the time it takes for one generation of workers to turn over. It does appear that polygyne queens are short-lived, even under "ideal" laboratory conditions (Oster and Wilson, 1978; Elmes, 1980).

The effect of survivorship of colonies (l_C) on the polygyny threshold is opposite to the effect of queen survivorship (Fig. 3A-L): as l_C increases, polygyny becomes more favored. Increased colony survivorship alone may be enough to select for polygyny. Polygyny appears to be correlated with longevity of nest sites in acacia-ant species (Janzen, 1973) and with colony survivorship in *Vespula* (Ross and Visscher, 1983).

The introduction of the red fire ant (*Solenopsis invicta*) has possibly provided a natural experiment concerning the effect of increasing colony survivorship on polygyny. This species was accidentally imported into the southern United States around 1940 and has spread rapidly, displacing the native species (Buren et al., 1974). In many regions, it has become the dominant species in open habitats, often producing very large populations (Wilson, 1971). In its native South America, the species has a much more restricted occurrence, probably due to an abundance of natural parasites (Lofgren et al., 1975), effective competitors (*Pheidole* spp.) and the predatory doryline army ants (Buren et al., 1974). A main effect of the ecological release experienced by imported *S. invicta* must be that colonies have longer

expected average lifetimes. This increased l_c for fire ant colonies may be selecting for polygyny. Polygyny has recently arisen apparently independently in several different areas, and within those areas, its frequency is increasing to the point of polygyny becoming locally common (Fletcher et al., 1980). The workers in polygyne colonies are smaller than those in monogyne colonies, but otherwise, individuals in the two types of colonies do not appear to differ morphologically. Both types of colonies are found in similar habitats, with no noticeable behavioral differences except for the willingness of polygyne colonies to accept multiple queens (Ross and Fletcher, 1985). Ross et al. (1987) found the monogyne and polygyne forms to be genetically indistinguishable and concluded that polygyny must have recently evolved from the monogyne population.

An important result of the model is that polygyny can reduce the number of sexuals per brood substantially and still be favored with certain combinations of l_c and l_Q (e.g., Fig. 3I, L). The gain in future reproduction due to polygyny can offset losses in present reproduction. Therefore, fitness comparisons of individuals in monogyne and polygyne colonies should involve lifetime reproduction (or at least several broods).

Several of the assumptions underlying the model can be examined in more detail. All queens were assumed to produce an equal proportion ($1/Q$) of the brood (assumption 2). Asymmetries in egg production could affect polygyny thresholds. If α queens, on average, produce more than $1/Q$ of the total offspring, polygyny is more likely, because the average sexual offspring has a higher relatedness to colony members. If α queens produce fewer than $1/Q$ of the total offspring, polygyny is less likely.

For mathematical simplicity, it is assumed that colonies produce equal numbers of males and females (assumption 4). However, it has been shown that workers in monogyne colonies tend to bias investment towards females (Trivers and Hare, 1976; Nonacs, 1986). Assuming that workers favor the production of sisters from their mother's eggs has no major effect on the model's predictions, other than slightly increasing the workers' polygyny threshold.

In terms of assumption 5, the addition of new queens after each brood matures may eventually result in colonies containing multiple generations of queens and workers, many of whom are only distantly related. This may explain why average relatedness between members of polygyne colonies in some species appears to be very low (Craig and Crozier, 1979; Pamilo, 1982; Pearson, 1982; Ross and Fletcher, 1985). However, the fact that low average relatedness may be the eventual result of continual queen addition does not alter the conditions that favor the preference of polygyny by the original workers. It should be noted that there are polygynous species that do show significant intracolony relatedness (Pamilo, 1982; Pamilo and Rosengren, 1984). The model predicts that there will be high relatedness among colony members when stable polygyny is first achieved. Over a colony's lifetime, however, this need not remain high but could, in fact, decline markedly. This suggests that understanding the dynamics of colony social systems may require repeated measurements of member relatedness over several generations of workers.

I assume that queens mate only once (monoandry). The influence of using more than one male's sperm (polyandry) on preferred queen number is unclear. Polyandry will reduce the average relatedness within broods, but workers should still favor aiding full sisters, if they can be identified. However, a cost could be associated with polyandrous queens in polygyne colonies. The average relatedness of progeny of increasingly polyandrous mothers to the workers will approach $1/4$ (most individuals are half-sibs). At this point, a worker would favor the replacement of its mother with a full sister, whose progeny will always be related to the worker by $3/8$, regardless of polyandry. It is interesting to note that polygyne species appear to be less likely to mate multiply than are monogyne species (Bartels, 1985).

I assume that any number of queens more than one imposes a constant cost on sexual production (assumption 6). It would be more realistic to have costs changing as a function of queen number. However, the shape of the curves would be greatly affected by the slope of the cost function. Specific cost functions due to increasing queen number are

unknown and, furthermore, are likely to vary considerably between species. Therefore in a general model, it is not particularly enlightening to add a nonconstant treatment of cost, although it should be realized that adding queens may incur brood-rearing costs and that these costs may set an upper bound on queen number. In contrast, if polygyny increases the output per brood ($c > 1$), it seems likely that polygyny will almost always be favored. Productivity could be increased in situations where colonies aggressively expand their territories and displace competitors by dispersing large groups of workers with queens to control these new areas (Rosengren and Pamilo, 1983).

The above models do not explicitly consider worker reproduction. However, the effects of polygyny are essentially equivalent to the production of males by unmated workers or the production of both sexes by mated workers (gamergates). The only difference involves whether the laying sisters are from the worker or queen castes. In both cases, as sexual production by sisters increases, the relatedness of the sexual offspring to the average worker approaches $\frac{1}{2}$.

Polygyny and Reproductive Success in Natural Colonies

Within the literature, there exist data sets from eight ant species that have a variable number of queens, with which it may be possible to compare reproductive success. I calculated reproductive success for an average worker in three classes of colonies: monogyne (1 queen), weakly polygyne (2–4 queens), and strongly polygyne (5 or more queens). In the calculations for monogyne colonies, I assume that all sexual offspring are full sibs of the workers. Therefore, the average worker in a monogyne colony has an expected reproductive success of

$$\left(\frac{1}{n}\right) \sum_1^n (0.25M + 0.75F) \quad (9)$$

where n is the number of colonies in the data set and M and F are the number of male and female sexuals, respectively. In

colonies with more than one queen, I assume that one queen is the mother of the other queens, which are full sisters of the original workers. All queens contribute equally to sexual production, and therefore, the average original worker in a multiqueen colony has the expected reproductive success given in Expression (10) below, where Q is the number of queens in the colony.

The results (Table 2) give the reproductive success an average worker can expect from a single brood in monogyne and multiqueen colonies. Note that the cost function (c) of polygyny from the previous models need not be calculated. The effects of polygyny are evident in the changes in reproductive success within single broods across the queen classes. Also, no assumptions about whether workers or queens control investment ratios are necessary. These results, however, are for only one brood [equivalent to $\bar{r}_1 c N_m$ in Eq. (7)] and do not include possible future reproduction. As such, only *Myrmica sabuleti* workers can expect greater success in multiqueen situations. In this species, therefore, polygyny may always be the better strategy, and monogyne colonies may exist only as a transient phase until new queens are added. In the other seven species, multiqueen colonies are at a disadvantage when only one brood is considered. For these species, the advantages of polygyny may be apparent only when lifetime fitness is calculated.

Lifetime fitness for colonies were estimated from (7) and (8), using the per brood reproductive data for each queen class and a wide range of values for l_Q and l_C . Relative fitnesses associated with polygyny to monogyne were calculated as for Figure 3 and are plotted in Figure 4 against a range of estimates for the probability of an average queen contributing eggs to the next brood (l_Q). As in the results presented in Figure 3 for all species, polygyny appears to be more selectively advantageous when estimates of colony survivorship are high and queen contributions to subsequent broods are low.

In all seven species, there are regions where either monogyne or polygyny is fa-

$$\frac{1}{n} \sum_1^n \frac{0.25M + 0.75F + 0.375(M + F)(Q - 1)}{Q} \quad (10)$$

TABLE 2. Reproductive success ($\bar{r}_1 c N_m$) of a worker from the average brood produced by monogyny, weakly polygyny (2–4 queens), or strongly polygyny (5 or more queens) colonies. Q = mean number of queens within each class, and n = number of colonies. The polygyny *Rhytidoponera* colonies contain gamergates (mated workers) and not true queens.

Species (references)	Monogyny		Weak polygyny			Strong polygyny		
	$\bar{r}_1 c N_m$	n	Q	$\bar{r}_1 c N_m$	n	Q	$\bar{r}_1 c N_m$	n
<i>Formica pallidefulva incerta</i> (Talbot, 1948)	42.15	5	2.67	12.03	3	11.20	12.10	5
<i>Leptothorax longispinosus</i> (Herbers, 1984)	4.12	54	2.63	3.73	27	6.58	3.51	17
<i>Myrmica ruginodis</i> (Brian and Brian, 1951; Mizutani, 1981; G. W. Elmes, pers. comm.)	113.37	15	2.33	81.36	6	13.20	40.60	5
<i>M. sabuleti</i> (Brian, 1972; G. W. Elmes, pers. comm.)	14.57	78	2.38	24.70	42	9.76	63.22	33
<i>M. schencki</i> (Talbot, 1945)	33.92	12	2.75	15.46	4	—	—	0
<i>M. sulcinodis</i> (Elmes, 1974, pers. comm.)	12.76	74	2.41	6.92	34	10.79	5.73	28
<i>Rhytidoponera chalybaea</i> (Ward, 1983a, 1983b)	29.08	31	4.00	12.67	55	—	—	—
<i>R. confusa</i> (Ward, 1983a, 1983b)	19.00	75	4.00	7.80	70	—	—	—

vored. However, for monogyny to be favored in *Leptothorax longispinosus*, the model requires an unlikely combination of high queen survivorship and very low colony survivorship (Fig. 4C, D). Therefore, this model alone cannot explain why monogyny appears to remain both common and stable over time (Herbers, 1984). It should be noted that the model's prediction of instability for monogyny is the opposite of the conclusions reached by Herbers (1984) from measuring alate production per queen in a given year. Increased monogyny appears to be an ecological response to the number of nest sites available. If new unoccupied nest sites are provided, colonies fractionate to exploit them (Herbers, 1986).

This analysis involved unavoidable assumptions about the degrees of relatedness between colony members. I examined the ideal kin-selection situation in which the queens consist of an original foundress and readmitted sisters of the workers. Obviously, if more distant relatives or unrelated individuals become queens, this will alter the calculations of reproductive success. For example, if *L. longispinosus* β queens are not full sisters, the advantages of polygyny may have been overestimated, and monogyny may be more stable than predicted by the model.

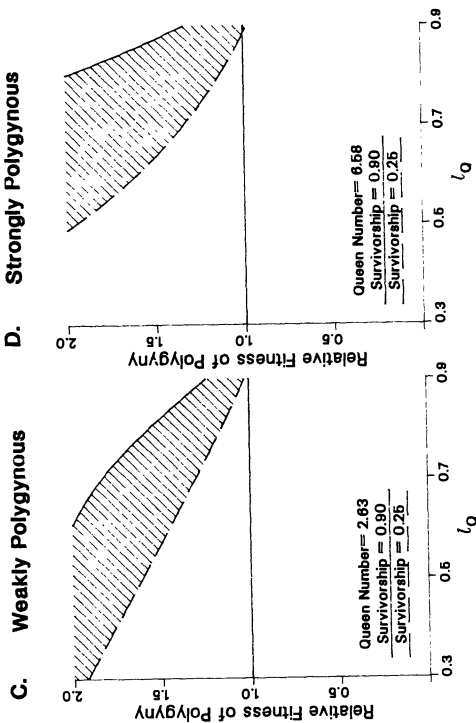
Coexistence of monogyny and polygyny strategies can be evolutionarily stable in a species if the combination of l_c , l_Q , and progeny per brood results in equal fitness across queen classes or if the values vary in

a heterogeneous environment so as to favor alternate strategies in different areas. Does the model predict these possible results with biologically reasonable values of l_c and l_Q ? Elmes (1980), modeling queen dispersion among *Myrmica* colonies, predicted that polygyny is favored in part by high queen mortality. To explain the observed patterns, he predicted gross annual mortality rates of between 11% and 50%. Within this range of l_Q values, the model predicts regions where monogyny or polygyny are favored as well as an isocline of equal fitness for all *Myrmica* species tested (Fig. 4E–I). Furthermore, in *M. ruginodis*, it appears that, as the model predicts, the monogyny form predominates in short-lived habitats (lower expected l_c), while the polygyny form is more prevalent in relatively stable habitats (Elmes, 1978; Brian, 1983).

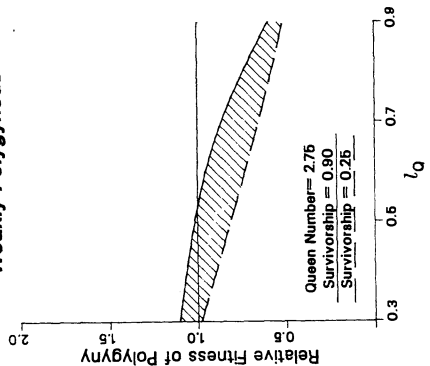
Conclusions

Queen number appears to be an adaptable trait within the eusocial Hymenoptera and seems to be explainable by a combination of kin-selection and ecological arguments. In perennial colonies, either monogyny or polygyny can be favored, depending upon the likelihood of any given queen contributing eggs to successive broods and the expected survivorship of the colony itself. Polygyny can be favored even when it reduces the number of sexual offspring produced per brood. Data from all eight species examined support the hypothesis that polygyny can be a kin-selected trait.

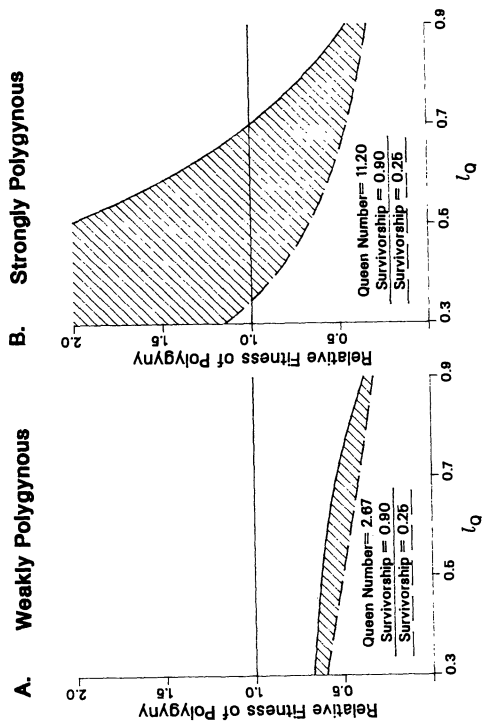
Leptothorax longispinosus



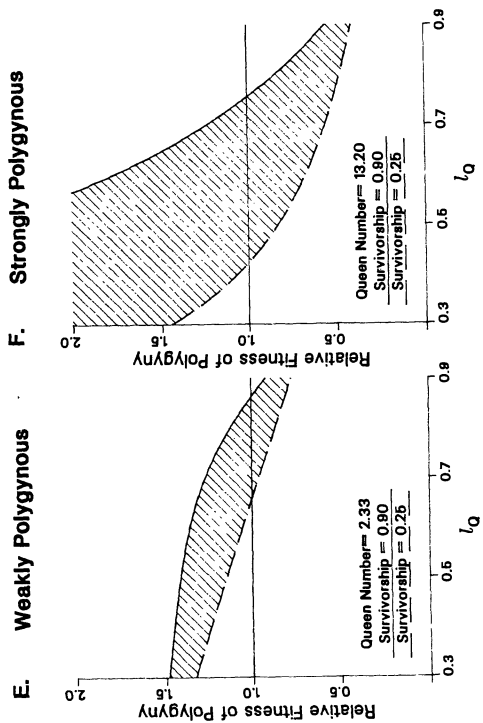
G. *Myrmica schenckii*
Weakly Polygynous



Formica pallidefulva incerta



Myrmica ruginodis



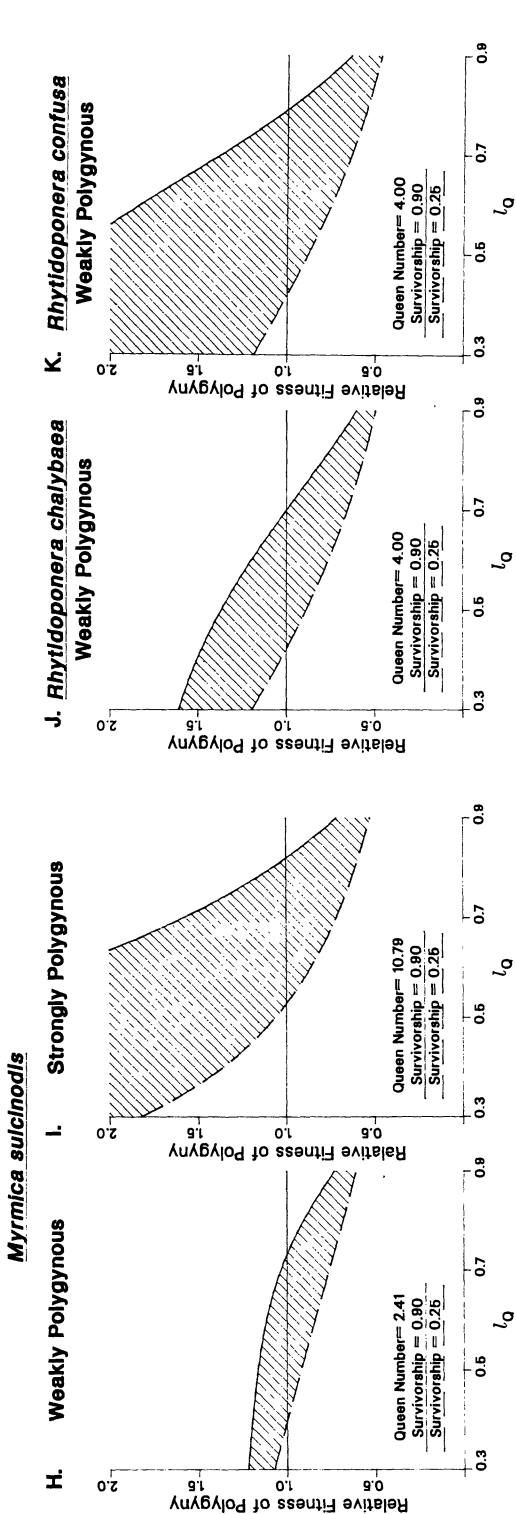


FIG. 4. Estimated colony fitness for seven ant species. The shaded areas between the curves represent the estimated fitness of polygynous colonies relative to monogynous colonies for a range of l_Q and l_C values. Polygyny is favored when relative fitness is greater than one. The polygynous *Rhytidoponera* colonies have gamergates (mated workers) instead of true queens.

Colonies are mutualistic, in the sense that most, if not all, members could not do better by abandoning the nest. However, within the colony, queens and workers may be in conflict over which individuals become the polygyne queens. Primary polygyny should be favored by foundresses, and secondary polygyny should be favored by their workers. If polygyny is favorable for both queens and workers, the optimal number of queens need not be the same for both castes. Therefore, it is probable that workers and queens cannot simultaneously maximize their fitness within any single polygyne colony.

Group or colony-level selection may favor polygyny, but these do not appear to be necessary to explain the phenomenon (cf. Oster and Wilson, 1978). Polygyny also does not appear to involve parasitism of established colonies by additional queens. If additional queens were colony parasites, polygyny should be deleterious for all colony members, except the parasitizing queens themselves. However, the estimated fitnesses of workers (Fig. 4A–K) suggest that they benefit from multiple queens. Although these mechanisms may explain polygyny in some species, kin selection is likely to be more influential in most species.

The models' results are in accordance with Hölldobler and Wilson's (1977) observations that polygyny tends to be associated with ephemeral nest sites that require frequent colony moves with increased chances of workers losing contact with queens (low l_Q in the models) or with stable, long-lived habitats (high l_Q). However, it may be too simple to assume that polygyne species may be characterized by a small set of ecological attributes. Habitat productivity, climate, and abundance of competitors and predators may all interact with the above factors to affect queen numbers. Therefore, neither monogyny nor polygyny may be always or even predictably affiliated with any particular type of habitat.

The models suggest that queen number may be an ecologically responsive trait. Evolutionarily, this may make it difficult to determine ancestral social systems. It has been postulated that monogyny is ancestral with polygyny being a derived state (Hölldobler and Wilson, 1977; Fletcher and Ross,

1985), that polygyny is ancestral, with monogyny being a derived state (West-Eberhard, 1978b; Elmes, 1980), and that a mixed strategy is ancestral, with strict monogyny and polygyny both being derived states (Ward, 1983a; Brian, 1983). I suggest that, within different genera, each scenario may be at times correct. The process, however, may be quite reversible, and as conditions change, the optimal queen number within a species may track those changes to maximize fitness. Therefore, it may be futile to classify monogyny or polygyny as generally being advanced or primitive, ancestral or derived for eusocial Hymenoptera as a group.

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